Fitness Consequences of Female Alternative Reproductive Tactics in House Mice (Mus musculus domesticus)

Ferrari, Manuela ; Lindholm, Anna K ; König, Barbara

Abstract: Alternative reproductive tactics (ARTs) are defined as discrete differences in morphological, physiological, and/or behavioral traits associated with reproduction that occur within the same sex and population. House mice provide a rare example of ARTs in females, which can rear their young either solitarily or together with one or several other females in a communal nest. We assessed the fitness consequences of communal and solitary breeding in a wild population to understand how the two tactics can be evolutionarily stable. Females switched between the two tactics (with more than 50% of all females having two or more litters using both tactics), pointing toward communal and solitary breeding being two tactics within a single strategy and not two genetically determined strategies. Communal breeding resulted in reduced pup survival and negatively impacted female reproductive success. Older and likely heavier females more often reared their litters solitarily, indicating that females use a condition-dependent strategy. Solitary breeding seems the more successful tactic, and only younger and likely less competitive females might opt for communal nursing, even at the cost of increased pup mortality. This study emphasizes the importance of analyzing phenotypic plasticity and its role in cooperation in the context of female ARTs.

DOI: https://doi.org/10.1086/700567

Fitness Consequences of Female Alternative Reproductive Tactics in House Mice (*Mus musculus domesticus*)

Manuela Ferrari,* Anna K. Lindholm, and Barbara König

Department of Evolutionary Biology and Environmental Studies (IEU), University of Zurich, Winterthurerstrasse 190, 8057 Zurich, Switzerland

Submitted April 7, 2017; Accepted August 15, 2018; Electronically published November 15, 2018

Online enhancements: appendix. *Dryad data:* https://dx.doi.org/10.5061/dryad.k1s0c7h.

ABSTRACT: Alternative reproductive tactics (ARTs) are defined as discrete differences in morphological, physiological, and/or behavioral traits associated with reproduction that occur within the same sex and population. House mice provide a rare example of ARTs in females, which can rear their young either solitarily or together with one or several other females in a communal nest. We assessed the fitness consequences of communal and solitary breeding in a wild population to understand how the two tactics can be evolutionarily stable. Females switched between the two tactics (with more than 50% of all females having two or more litters using both tactics), pointing toward communal and solitary breeding being two tactics within a single strategy and not two genetically determined strategies. Communal breeding resulted in reduced pup survival and negatively impacted female reproductive success. Older and likely heavier females more often reared their litters solitarily, indicating that females use a condition-dependent strategy. Solitary breeding seems the more successful tactic, and only younger and likely less competitive females might opt for communal nursing, even at the cost of increased pup mortality. This study emphasizes the importance of analyzing phenotypic plasticity and its role in cooperation in the context of female ARTs.

Keywords: alternative reproductive tactics, communal nursing, wild house mice.

Introduction

Reproductive success is a major component of an individual's fitness. Understanding what causes its variation and how an individual may maximize its lifetime reproductive success is therefore crucial. In many species, especially those living in groups, reproductive skew can be observed, with a few individuals largely monopolizing reproduction (Hager and Jones 2009). High reproductive competition and variance in reproductive success may lead to the evolution of alternative life-history trajectories within the same population, with individuals using alternative ways to optimize their reproductive success (Brockmann et al. 1979).

Alternative reproductive tactics (ARTs) are defined as discrete differences in morphological, physiological, and/or behavioral traits associated with reproduction that occur among individuals of the same sex and population (Gross 1996; Taborsky et al. 2008). A specific tactic expressed by an individual is the result of its underlying genetically determined strategy (i.e., the decision rule). A tactic can be fixed for a given strategy with some individuals using one genetically determined strategy (therefore expressing one tactic) and other individuals using an alternative strategy and consequently expressing a different tactic (Gross 1996). However, ARTs can be expressed as a consequence of one single strategy in the population. Such a single strategy can be either a mixed strategy, with individuals expressing a tactic based on a probabilistic decision rule, or a conditional strategy, with the decision linked to an individual's condition or status. ARTs within a single strategy can be fixed over an individual's lifetime or change between or even within breeding attempts (Gross 1996). Genetically polymorphic alternative strategies are expected to be evolutionarily stable only when they on average result in similar fitness or are negatively frequency dependent (Shuster and Wade 1991), while ARTs (within a single strategy) can also be evolutionarily stable even if they vary in fitness outcome.

ARTs were hypothesized to have a higher prevalence in males because high intrasexual variation in fitness is more commonly found in males and females usually cannot avoid high allocation into reproduction (egg production, gestation, etc.; Taborsky et al. 2008). In agreement with this prediction is the large number of ARTs described for males in many different species (Brockmann 2008; Shuster 2008).

* Corresponding author. Present address: Department of Wildlife Ecology and Conservation, University of Florida, 362 Newins-Ziegler Hall, Gainesville, Florida 32611; email: manuela.ferrari@ieu.uzh.ch.

ORCIDs: Ferrari, http://dx.doi.org/0000-0003-4610-2806; Lindholm, http://dx.doi.org/0000-0001-8460-9769.

Am. Nat. 2019. Vol. 193, pp. 106–124.
DOI: 10.1086/700567

More recently, however, increasing focus on female competition revealed evidence for the existence and importance of ARTs in females (Taborsky et al. 2008; Clutton-Brock 2009; Stockley and Bro-Jørgensen 2011). Typical ARTs described for females include conspecific brood parasitism (Yom-Tov 1980; Yanagisawa 1985; Field 1992; Zink 2003), the exploitation of nests built by female conspecifics (Brockmann et al. 1979; Field 1994), and joint versus solitary breeding (Scott and Williams 1993; Schradin et al. 2012; Hill et al. 2015).

House mice (*Mus musculus domesticus*) provide an example for ARTs in females. House mice typically live in social groups, usually consisting of one dominant male, several reproducing females, and sometimes also nonreproducing individuals (Lidicker 1976; König and Lindholm 2012). Breeding females in such groups can either rear their young solitarily or pool litters in a communal nest, a behavior that has been observed both under laboratory and natural conditions (Sayler and Salmon 1969; Wilkinson and Baker 1988; König 1993; Weidt et al. 2014). House mice often associate with related individuals (König et al. 2015), and communal nursing preferentially occurs among relatives (Wilkinson and Baker 1988). However, in a free-living population only 12.6% of breeding females had other breeding females from their natal group (littermates or nest mates) available as potential partners for communal breeding (Harrison et al. 2018). Females were more likely to engage in communal breeding when the general relatedness in their social group was high, even though pairwise relatedness did not directly predict with which available partner in their group they formed a communal litter (Harrison et al. 2018). In laboratory studies, females also communally nursed with unrelated and unfamiliar females (König 1994*b*; Ferrari and König 2017).

In a communal nest, litters often differ by a few days in age. Once the second female has given birth and combined her offspring with the already-present litter, both mothers will nurse all pups indiscriminately (Ferrari et al. 2015) and are apparently unable to distinguish between their own and others' offspring (Chantrey and Jenkins 1982; König 1989; Manning et al. 1995). Communal offspring care was shown to increase female lifetime reproductive success in the laboratory, with communally nursing sisters weaning a higher number of pups over an experimental life span of 6 months than solitarily nursing females (König 1994*a*). There is further evidence for increased survival of pups reared communally in a seminatural population (Manning et al. 1995) as well as in a natural population through polyandry-driven reduction in male infanticide (Auclair et al. 2014). However, free-living females were observed to rear offspring solitarily even when the option to join the litter of another female was available (Weidt et al. 2014), indicating that females might not always benefit from pooling their litters. Laboratory studies further revealed costs of communal nursing and a scope for exploitation. If females varied in litter size, they benefited unequally, with the mother of the larger litter exploiting her partner because of indiscriminate milk production and nursing (Ferrari et al. 2015). Additionally, several laboratory studies reported that communally breeding females killed some pups of their partner when highly pregnant, shortly before they gave birth themselves (König 1994*a*; Palanza et al. 2005; Schmidt et al. 2015; Ferrari et al. 2016).

Understanding the evolution and maintenance of ARTs requires information about their fitness consequences. Few empirical studies have analyzed the fitness of individuals using alternative tactics in natural populations for males (Lank et al. 1995; Brown and Brown 1998; McGuire and Getz 2010; Schradin and Lindholm 2011) and females (Lyon 1993; Brown and Brown 1998; Ahlund and Andersson 2001; Zink 2003). Most studies quantifying the fitness of female ARTs focused on birds, with very little data on mammals. We aimed to (i) quantify the occurrence of two female ARTs in a wild population of house mice and (ii) calculate the associated fitness consequences. Data from a long-term study allowed us to follow individual females over their lifetime, document what tactic they used, and analyze the consequences of a specific tactic for the females' reproductive success. If communal and solitary nursing are two genetically determined alternative strategies, we expect females not to be able to switch tactics during their lifetime. Two strategies would further need to have equal fitness to be evolutionarily stable. Information about whether the two alternative tactics are plastic or fixed during a female's lifetime and how they affect female fitness could therefore help us to understand whether communal and solitary breeding are two genetically determined strategies or instead one strategy with two tactics that could either be condition dependent or based on a probabilistic decision rule. Taken together, this approach will contribute to our understanding of the conditions that favor the evolution and maintenance of female ARTs.

Methods

Study Population

We used data collected as part of a long-term project on wild house mice, located in a barn close to Illnau, Switzerland. A free-living house mice population was set up in a barn in 2002 and has been intensively studied ever since (for a detailed description, see König and Lindholm 2012). The barn is closed against larger predators but allows house mice (or other small animals) to enter and leave freely. When leaving the building, house mice risk predation by several mammals and birds (such as cats, foxes, owls). The population is exposed to parasites and to diseases (Dobay et al. 2015). Wooden and plastic barriers structure the 72-m^2 barn into four major

sections that nevertheless can be crossed by the house mice through holes. Food, water, and nest-building material (straw and hay) are provided ad lib. at several places throughout the barn. Forty artificial nest boxes (10 per sector) serve as breeding sites for the house mice, and bricks, boards, sticks, and plastic tubes provide additional shelters. The population setup is intended to resemble the natural habitat of commensally living house mice in middle Europe, which is why the house mice in this free-living population are not restricted in food access. Data used for this study have been deposited in the Dryad Digital Repository: https://dx.doi.org/10.5061/dryad.k1s0c7h (Ferrari et al. 2018).

All adult and subadult house mice were regularly captured (every 6–8 weeks) and their sex, weight, and reproductive status (for females, whether they are pregnant or lactating) were documented. During such population monitoring, adults of minimally 18 g were injected with a transponder (RFID tag; Trovan ID-100A implantable microtransponder: weight, 0.1 g; length, 11.5 mm; diameter, 2.1 mm) for individual identification, and a tissue sample (ear punch) was collected for genotyping and pedigree analyses. All house mice found dead in and around the study site were recorded, and tissue samples were taken for genetic analyses. Capturing all individuals at regular time intervals allowed us to estimate the population size. Tagging of adults further allowed regular documentation of their presence in the barn, either in nest boxes or in shelters (with the help of handheld readers or by an automatic antenna reading device attached to each entrance to the nest boxes; for details, see König and Lindholm 2012; König et al. 2015). All tagged adults regularly visited and used several neighboring nest boxes, where they met with conspecifics. Social network analyses based on individual meetings within nest boxes revealed that house mice lived in socially closed groups (individuals did not visit nest boxes used by members of neighboring groups). In 2013 and 2014 we documented 10–12 social groups in the barn (König et al. 2015; Lopes et al. 2016). The readings from the automatic antenna device further enabled us to determine for those adults that were not found dead the last day they had been recorded in a nest box. We assumed that they had left the barn afterward or had died without us finding the carcass.

Monitoring Reproduction

The 40 nest boxes and all shelters were checked at least every 13 days for the occurrence of new litters. All litters born and documented between January 1, 2007, and December 31, 2011, were used for this study (data from earlier years had to be excluded because of a slightly different data collection protocol, and data from later years had to be excluded because parentage analyses had not yet been finalized at the time of analysis). Pups found were aged (on the basis of morphological traits; see König and Lindholm 2012) and weighed, and each litter was given a unique code (LitterID). Since 2008 litters found at an age of 10 days or younger were tattooed in one or several paws (colored toe tattoo; Aramis Microtattoo Systems) to facilitate later identification. Litters were revisited when pups were 13 days old to collect data on the number of living pups and their body mass and to take a tissue sample (ear punch) for maternity analyses. To minimize disturbance, we immediately sampled litters that were found for the first time when pups were older than 10 days (ear samples can be obtained only from pups 11 days or older), and we took pup body mass and body measurements. Ideally, pups would be sampled at the onset of weaning (day 17), since the body mass at that age would represent maternal allocation through milk. However, because pups open their eyes at day 14 and start becoming mobile (Mikesic and Drickamer 1992), they had to be sampled beforehand not to risk being unable to find and/or identify them.

We further recorded whether a litter was found alone in the nest box (solitary) or communally with one or several other litters in the same nest box. A nest was defined as communal when it contained pups we morphologically assigned to separate litters since they differed in age by at least 1–2 days. Nevertheless, genetic analysis (see below) was used to confirm maternity of all pups. Litters sharing the same nest box or shelter were always communal, as the confined space in a nest box did not allow for occupancy by two or more solitary litters. Some communal nests were detected only after genetic analyses because pups were too similar in age to be distinguished otherwise. We refer to such litters as cryptic communal nests. Not all litters were found in the same nest box at sampling as when first found because females sometimes moved litters after having been disturbed (own observations), which is why we did not search for litters more regularly. We documented whether a litter was relocated to a different nest box or shelter between the date it was first found and sampling.

House mice start eating solid food when they are 17 days old and are weaned at an age of 21–23 days. All pups of at least 17 days were therefore considered subadults and were no longer considered as part of a communal nest (this definition has been used in other studies; see König 2006; Weidt et al. 2014).

This particular population of house mice produced litters during almost all months of the year but nevertheless varied seasonally in reproductive activity. The majority of litters were produced during the warmer months (April–September; König and Lindholm 2012), which consequently also resulted in a fluctuating population size. Data collected during population monitoring events were used to estimate population size in a given month, and temperature (°C) in the barn was constantly documented to calculate monthly means.

Parentage Analyses and Pairwise Relatedness

Parentage analysis was conducted using markers at 25 polymorphic microsatellite loci (markers: Chr1_20, D2Mit145, D3Mit278, D4Mit227, Chr5_20, D5Mit122, D5Mit352, D6Mit139, D6Mit390, D7Mit17, D7Mit319, Chr8_3, D8Mit115, D9Mit-201, Chr10_11, D10Mit230, D11Mit150, D11Mit90, Chr12_2, D12Mit91, D13Mit-88, D14Mit44, D16Mit139, D18Mit194, and Chr19_17; Bult et al. 2007; Teschke et al. 2008). The program CERVUS 3.0 was used to assign a mother to each pup (Kalinowski et al. 2007). All females recorded in the barn in the 30 days prior to the birth of a pup were included as potential mothers. Each pup was further assigned a GeneticLitterID, which grouped same-aged pups sharing the same mother and allowed determining litter size at sampling.

Of the 797 litters from which pups were sampled, pups from 730 litters were assigned a mother with a certainty of 95% or more. Because of a rather high number of unassigned pups in the remaining litters, when using this conservative threshold we additionally included 67 litters that contained one or several pups that were assigned to a mother only with a confidence of at least 80% (while the remaining pups of the litter were assigned with a confidence of 95% or higher). A total of 123 pups could not be assigned to a mother, resulting in a slight underestimation of the litter size at sampling. Furthermore, for 451 pups found dead or alive it was not possible to determine whether they were found for the first time or belonged to a litter we had seen before because of contradicting tattoos, age estimates, or the number of pups. We omitted those pups from most of the analyses to avoid including them twice in different categories, again leading to an underestimation of the number of pups sampled in the population. Those pups were, however, included when we looked at the total number of pups sampled per female.

Not all litters could be used for all analyses because we did not have complete information for all of the factors of interest. Detailed sample sizes will be given for each analysis when we present the respective results.

We used the same 25 markers to calculate the Wang coefficient (Wang 2002) of pairwise relatedness among adult females in our data set with the software Coancestry (Wang 2011; https://www.zsl.org/science/software/coancestry). It allowed us to calculate the pairwise relatedness of two females relative to the genetic similarity between all females found in the reference population. All females alive in a given year were used as reference population. The analysis was done for each year separately to avoid calculating pairwise relatedness values for females whose life spans did not overlap. See Harrison et al. (2018) for a more detailed description and an explanation for why we used the Wang estimator for this particular population.

Statistical Analyses

We used Skew Calculator 2003 (https://www.eeb.ucla.edu/Faculty/Nonacs/pi.html) to calculate the binomial skew index (*B*; Nonacs 2000, 2003) for each communal nest (for which we knew the identity of all mothers involved) to test for inequality among females concerning the number of sampled pups they contributed. Negative *B* values indicate that females were more similar in their contribution to the communal nest than expected by chance (based on the variance in contributions among all females), revealing an egalitarian situation during indiscriminate nursing of the combined litters. Positive values indicate a pronounced nonegalitarian (rather despotic) situation, where one female contributed considerably more pups to the communal nest than the partner(s). Values that do not differ from zero suggest that the observed distribution in reproductive output within communal nests did not differ from random expectation.

The remaining statistical analyses were performed with R version 3.0.2 (R Core Team 2015). We conducted (generalized) linear models ([G]LMs) or (generalized) linear mixed models ([G]LMMs). The latter were used for dependent data (several litters born to the same female). (G)LMMs were performed with the package lme4 (Bates et al. 2014). Fulfilment of model assumptions were inspected visually, and if necessary data were transformed or the appropriate link function was chosen. GLMs and GLMMs with a binomial error distribution were tested for overdispersion. We further calculated variance inflation factors to test for problematic collinearities. The population size and the monthly mean temperature in the barn were included as covariates in all analyses, to control for a potential effect of seasonality on the factors of interest.

We started with the full model containing all biologically relevant parameters and used the dredge function in the package MuMIn (Bartoń 2014) to calculate all possible models containing those or fewer variables. Models were ranked according to their AICc (Akaike information criterion corrected for small sample size) values, and we used an information-theoretic approach to account for uncertainty in model selection and parameter estimation. Following Grueber et al. (2011), we obtained averaged parameter estimates (full average) by averaging across all models within 4 ΔAICc of the best model using Akaike weights (w). We used the relative importance in the averaged model and the confidence interval of the averaged parameter estimates to assess the significance of fixed factors.

Ethical Notes

Data collection as well as all procedures and protocols involved in monitoring the population were approved by the

Veterinary Office, Zurich, Switzerland (licences 215/2006 and 51/2010).

Results

ARTs or Strategies?

We analyzed the occurrence of communal and solitary breeding during a 5-year period. In total, 1,279 litters were recorded in the barn. From 797 of those litters we sampled pups (alive) when they were approximately 13 days old (mean age ± SE, 13.0 ± 0.07 days), which we used as a proxy for survival until weaning. Furthermore, we sampled pups found dead from another 47 litters. In total, 358 females contributed to the 844 litters we genetically analyzed successfully (alive or dead). The 797 litters sampled on day 13 contained 3,303 living pups, with pups belonging to 963 genetically distinct litters (with unique GeneticLitterIDs). Cryptic communal nests (litters that contained pups from more than one GeneticLitterID) were relatively frequent, with 20% of all litters first described as solitary (based on morphology of pups) revealed to be cryptic communal nests after genetic analyses, and 27% of all communal nests contained more litters than we had assumed from differences in morphology among pups.

Females gave birth to between one and nine litters, with 30% of the females having only one litter. Of all the females that reproduced more than once, 93 (38%) reared all their litters communally, 19 (8%) had only solitary litters, and 134 females (54%) used both ARTs. Our data set allowed us to document the breeding behavior of several daughters from mothers of known reproductive phenotype. Note that sample sizes are rather small because of the low number of daughters that produced at least two litters within the study period. We analyzed the behavior of daughters whose mothers reared only solitary litters ($n = 9$). Of these, one (11%) also raised all her litters solitarily, like her mother; three (33%) raised all their litters communally; and the remaining five (56%) raised litters both solitarily and communally. Daughters of females that reared all their young communally ($n = 45$) were observed to do the same as their mother in 53% of cases, while 9% raised all litters solitarily and 38% had both solitarily and communally raised litters.

During the 5-year study period, we sampled pups (alive) from 963 genetically distinct litters (different GeneticLitterIDs) that originated from 350 different females. A total of 662 (69%) of the 963 litters were sampled in a communal nest (found in the nest together with at least one other litter at sampling), 297 (31%) were sampled solitarily, and for 4 we did not have information about their nesting condition at sampling. The proportion of litters sampled communally increased slightly over the years (see fig. 1).

Equal Fitness for Communal and Solitary Breeding?

Female Reproductive Success. We calculated reproductive success for all females born between 2007 and 2011 that reached adulthood (being tagged) and died or were last seen in the barn before the end of 2011 ($n = 500$). A total of 159 (31.8%) of the females were found dead; for the other females we do not know with certainty whether they dispersed, died inside the barn and were not found, or died outside the barn. As a result, our measure for female life span is only an approximation and corresponds to the time a female spent in the population. Here we define a female's reproductive success as the number of pups weaned (sampled alive) during the time she was observed in the population. For 249 (49.8%) of the 500 females, zero offspring reached sample age (around day 13); for the remaining 251 females, we sampled between 1 and 39 pups during their life span in the barn (see fig. A1; figs. A1–A4 are available online).

In the following, we focus only on reproducing females (females that weaned at least one offspring), analyzing in more detail the factors that might potentially affect the variation in reproductive success observed among females. We also used that data set to test whether females using communal or solitary breeding differed in fitness. As a measure for the tactic a female used during her lifetime, we quantified what proportion of litters she raised communally and included this as an explanatory variable, with the response variable being the square root of a female's reproductive success (number of offspring sampled alive during her lifetime). Further covariates were the population size and the mean temperature during the month the female was born, her body mass at tagging (an approximation for her body condition before the onset of reproduction), her age at first reproduction, and her total life span (the time she was observed in the barn). Our data set comprised 212 females that produced between 1 and 39 pups. We had to exclude the remaining females from the analyses because we did not have information on all the factors of interest. Our measure for reproductive success only included offspring for which we knew how they were raised (communally or solitarily) and might therefore be a slight underestimation of a female's reproductive success.

Model selection revealed that life span in the barn had the strongest effect on female reproductive success, with longer-lived females producing a higher number of offspring (table 1; fig. 2*A*). Furthermore, we found that with a higher proportion of a female's litters being raised communally, she had a lower lifetime reproductive success (table 1; fig. 2*B*). Communal and solitary breeding consequently did not result in equal fitness.

Likelihood to Have a Subsequent Litter and the Interbirth Interval. Whether a female raised a litter solitarily or communally had no detectable effect on the mother's likelihood

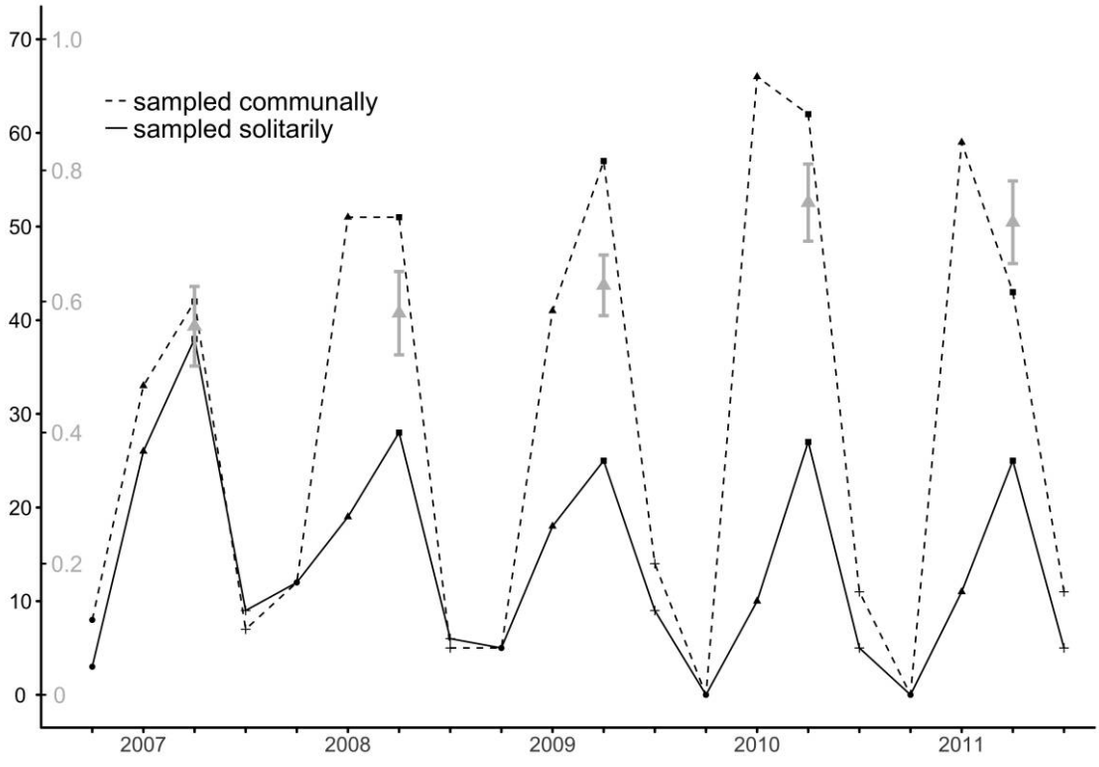

Figure 1: Number of solitary litters and litters that were part of a communal nest at sampling per season (spring: March to May [circles]; summer: June to August [triangles]; autumn: September to November [squares]; winter: December to February [plus signs]) for all 5 years of the study period. The proportion of all litters raised communally for each year is shown in gray (mean ± SE).

to give birth to another litter (table A1; tables A1–A4 are available online; $n = 789$ litters), nor did a female's tactic affect her interbirth interval (table A2). Females were more likely to produce another litter the younger they were and when their current litter was born during times of lower population density and lower temperature (table A1). Younger mothers also had shorter interbirth intervals, but the mean temperature in the barn and the population density had no detectable influence on a female's interbirth interval (table A2). On average, the interbirth interval was 66.7 ± 2.8 days (mean ± SE), ranging from 19 to 309 days ($n = 454$ pairs of litters).

Survival Differences of Pups Raised Communally and Solitarily. We analyzed pup survival in all litters that were found at least once before sampling, allowing us to calculate the proportion of pups surviving to sampling compared with the litter size when first found. If all pups of a litter died before sampling (i.e., were never found again), we were unable to assign them to a mother and therefore had to exclude them from the analyses. Omitting all litters with zero survival resulted in an overestimation of survival rates. We included an analysis of a litter's resampling probability as a way of estimating survival probabilities (fig. A2; table A3). Furthermore, all litters that were first found at sampling and all cryptic communal nests had to be excluded from the analyses because we were unable to determine litter size when first found and consequently to calculate the proportion of pups surviving until sampling. A total of 340 litters remained in the data set.

The tactic used by a female influenced pup survival, with the highest survival observed for solitarily reared litters (both solitary when first found and at sampling) and litters that turned solitary (communal when first found and solitary at sampling; such a situation mainly occurred because the older litter was weaned and had left the nest, and on occasion it occurred because all pups of one litter had died; table 2). A smaller proportion of pups survived from litters that were initially found solitary but communal at sampling or always communal. Additionally, we found that smaller and older litters when first found had a higher survival probability (table 2), while movements from one nest box to another between the two sightings reduced a

Table 1: Model summary statistics for the factors influencing female reproductive success

	Intercept	Population size	Life span	Mean temp	Age first reproduction	Tactic	Mass	df	AICc	ΔAICc	*w*
Model 1	**2.895**	−	**1.290**	−	**−.260**	**−.337**	−	**5**	**582.7**	**.00**	**.195**
Model 2	**2.895**	**−.167**	**1.249**	−	**−.230**	**−.316**	−	**6**	**583.3**	**.56**	**.147**
Model 3	**2.895**	**−.206**	**1.167**	−	−	**−.317**	−	**5**	**583.9**	**1.21**	**.106**
Model 4	**2.895**	−	**1.205**	−	−	**−.344**	−	**8**	**584.2**	**1.52**	**.091**
Model 5	**2.895**	−	**1.290**	**−.060**	**−.238**	**−.336**	−	**6**	**584.7**	**1.93**	**.074**
Model 6	**2.895**	−	**1.291**	−	**−.261**	**−.336**	**−.008**	**6**	**584.8**	**2.11**	**.068**
Model 7	**2.895**	−	**1.222**	**.137**	−	**−.341**	−	**5**	**585.2**	**2.52**	**.055**
Model 8	**2.895**	**−.171**	**1.253**	−	**−.233**	**−.315**	**−.030**	**7**	**585.4**	**2.65**	**.052**
Model 9	**2.895**	**−.163**	**1.250**	**−.017**	**−.225**	**−.316**	−	**7**	**585.4**	**2.69**	**.051**
Model 10	**2.895**	**−.180**	**1.182**	**−.084**	−	**−.319**	−	**6**	**585.7**	**2.95**	**.045**
Model 11	**2.895**	**−.206**	**1.167**	−	−	**−.317**	**−.003**	**6**	**586.1**	**3.33**	**.037**
Model 12	**2.895**	−	**1.202**	−	−	**−.344**	**−.027**	**5**	**586.3**	**3.57**	**.033**
Model 13	2.895	−	1.293	.062	−.240	−.336	−.016	7	586.8	4.06	.026
Model 14	2.895	−.209	1.257	−	−.232	−	−	5	587.1	4.33	.022
...											
Model 64	2.895	−	−	−.028	.182	−	.168	5	663.1	80.33	.000
Averaged parameters:											
Estimate[a]	2.90	−.08	1.24	−.02	−.15	−.33	−.0				
Unconditional SE	.06	.13	.14	.08	.16	.13	.06				
Lower 95% CL	*2.77*	−.34	*.96*	−.17	−.47	*−.58*	−.12				
Upper 95% CL	*3.02*	.17	*1.53*	.13	.17	*−.07*	.12				
Relative importance	−	.46	1	.24	.62	1	.20				

Note: The square root of the number of pups sampled over a female's lifetime (reproductive success) was used as the response variable in a linear model. Models within 4 AICc (Akaike information criterion corrected for small sample size) units of the best model are highlighted in bold and were used to calculate averaged effect sizes. Statistically significant confidence intervals (not crossing zero) are emphasized in italic. Factors included are defined as follows: population size = number of adults present in the barn during the month a female was born; life span = time between birth of a female and her death or until she was last seen in the barn; mean temp = mean temperature in the barn during the month a female was born; age first reproduction = a female's age when she first gave birth to pups that were genetically analyzed; tactic = the proportion of own litters a female raised communally; mass = a female's body mass at tagging as an indicator for her condition before first reproduction. Minus signs indicate that the model does not contain the factor. CL = confidence limit; *w* = relative model weights.

[a] Standardized on 2 standard deviations, following Gelman (2008).

litter's survival probability (fig. 3*A*; table 2). Population density and the mean temperature during the month in which a litter was born did not affect the proportion of pups surviving (95% confidence intervals [CIs] of their estimates crossed zero; table 2).

Both solitarily reared litters and litters that turned solitary were characterized by not being joined by another litter until sampling. We therefore decided in a second step to analyze whether the number of additional new litters a focal litter was found with at sampling influenced pup survival. With each litter added to the nest until sampling, pup survival decreased (fig. 3*B*; table 2). Whether a litter was solitary or communal when first found had no detectable effect on a litter's survival rate. Similarly to the first analysis, population size and mean temperature during the month a litter was born had no strong effect on pup survival, while relocation to a different nest box and decreasing pup age reduced survival rates.

Recruitment Rate. For all the litters that were sampled, we analyzed the proportion of pups that were later caught and tagged as adults in the population ($n = 589$ litters). Since pups may have dispersed as subadults, this does not perfectly reflect survival until adulthood but rather what proportion of a litter was recruited into the population. However, given the likely low survival rate of dispersing house mice, we are confident that the measure is a valid estimate of survival until adulthood. The analysis revealed that the status at sampling (communal vs. solitary) had no influence on the proportion of a litter recruited into the population (relative low importance of 0.30, compared with the population density and temperature—relative importance of 1 each—as estimated by the model-averaging approach). The number of recruited adults increased with decreasing mean temperature and increasing population density in the barn during the month of birth of the litter (table 3). Furthermore, adults originating from larger litters had a higher probability to be recruited into the population (table 3).

Reproductive Skew among Communally Nursing Females. We analyzed 77 communal nests that contained between

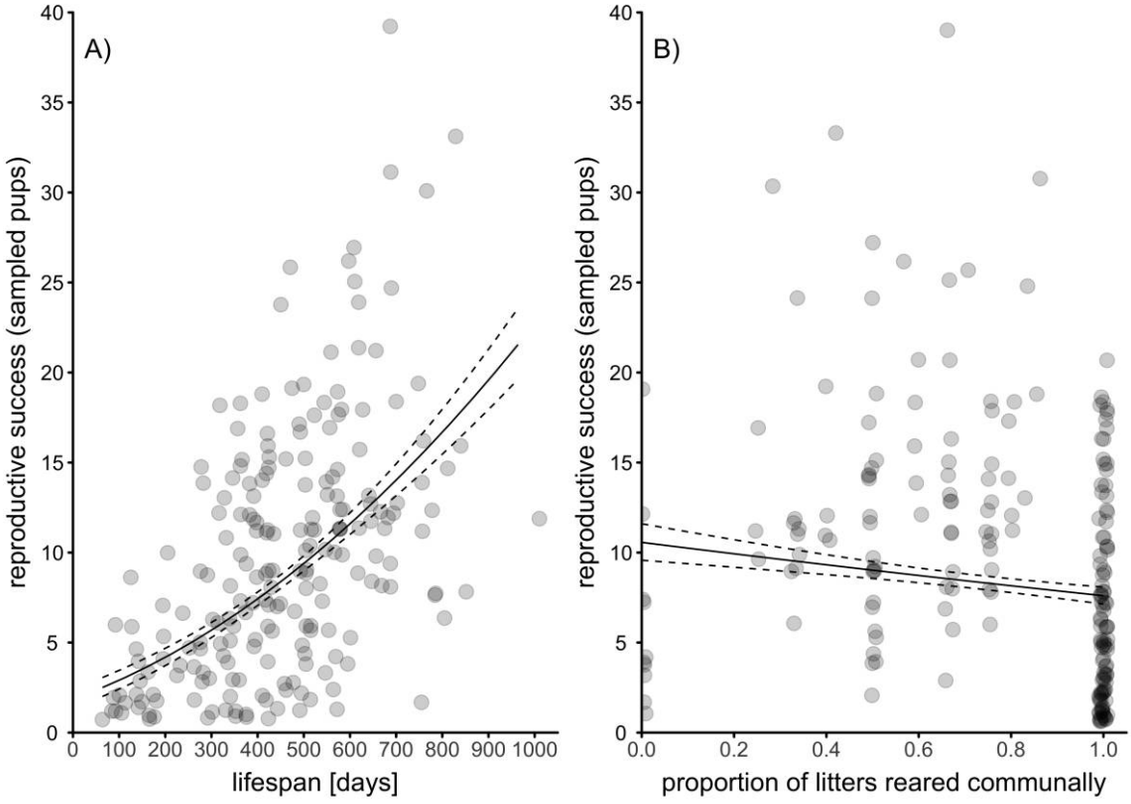

Figure 2: Female reproductive success (number of offspring sampled on day 13) in relation to her life span (i.e., the time she was observed in the population; *A*) and the proportion of litters a female reared communally (*B*). Plotted are model estimates (mean ± SE) obtained from model averaging of linear models. Gray dots represent raw data ($n = 212$ females).

two and four litters, with on average 2.2 ± 0.05 (mean ± SE) females contributing to it. The binomial skew index (B) averaged over all litters in communal nests did not differ from zero ($B = 0.0004$, $P = .48$), indicating that the observed variation in female contribution did not differ from random expectation. We nevertheless tested whether the average pairwise relatedness among females sharing a communal nest influenced the amount of skew we observed. If three or more females contributed to a communal nest, we took the average of all pairwise relatedness values. We further included the maximal age difference between the pups (age of oldest litter minus age of youngest litter) because a higher reproductive skew might be expected if pups differ in age, as killing younger pups before joining a communal nest might be easier. Additionally, we included the age difference between the females (age of oldest female minus age of youngest female) to test whether a larger age difference between females—and therefore likely also a larger weight difference—might indicate that one of the females was dominant over the other. None of the variables, however, influenced the B index (table 4). The age difference between the litters had the highest importance of all the variables (0.48) but still did not detectably influence skew (95% CI crossed zero). Females rearing their litters communally had on average a relatedness of 0.28 (mean Wang estimate of pairwise relatedness; 95% CI: 0.22–0.34). In this study population, a Wang estimate of 0.28 equals a pedigree relatedness value of 0.25, as among half-siblings (see Harrison et al. 2018).

Conditional ARTs?

We analyzed whether female age at the time she gave birth to a litter, the mean temperature in the barn, or the population density during the month the litter was born influenced the probability that a litter was raised solitarily or communally. Some litters had to be excluded (96 litters) because pups from a single litter were sampled from several nest boxes, indicating that pups from a nest were moved but not all together, which could result in some genetic littermates being raised communally while others were raised solitarily in another nest box. We furthermore

Table 2: Model summary statistics for the proportion of pups surviving until sampling

	A. Female tactic treated as a categorical variable												
		Rearing condition											
	Intercept	sol to com	purely com	com to sol	Relocation	Population size	Age first	ls first	Mean temp	df	AICc	ΔAICc	*w*
Model 1	**2.033**	+			+	−	**.742**	**−.475**	−	**9**	**981.6**	**0**	**.383**
Model 2	**2.018**	+			+	**.267**	**.753**	**−.477**	−	**10**	**982.5**	**.90**	**.244**
Model 3	**2.043**	+			+	−	**.750**	**−.476**	**−.105**	**10**	**983.3**	**1.75**	**.159**
Model 4	**2.052**	+			+	**.331**	**.764**	**−.481**	**−.160**	**11**	**983.8**	**2.22**	**.126**
Model 5	1.903	+			+	−	.814	−	−	8	987.1	5.48	.025
Model 6	1.890	+			+	.256	.826	−	−	9	988.0	6.43	.015
Model 7	1.912	+			+	−	.821	−	−.94	9	988.9	7.29	.010
Model 8	1.898	+			+	.316	.837	−	−.149	10	989.4	7.83	.008
...													
Model 64	1.440	−			−	.392	−	−	−.132	5	1,030.5	48.86	.000
Averaged parameters:													
Estimate[a]	2.03	−.66	−.62	.02	−.56	.12	.75	−.48	−.04				
Unconditional SE	.20	.22	.21	.28	.17	.21	.18	.17	.11				
Lower 95% CL	*1.64*	*−1.10*	*−1.03*	−.53	−.89	−.30	*.39*	*−.82*	−.26				
Upper 95% CL	*2.42*	*−.23*	*−.22*	.56	−.22	.54	*1.11*	*−.13*	.18				
Relative importance	−	1			1	.41	1	1	.31				

	B. Female tactic analyzed as the number of additional litters joining a nest											
	Intercept	No. new litters	Status first	Relocation	Population size	Age first	ls first	Mean temp	df	AICc	ΔAICc	*w*
Model 1	**1.753**	**−.499**	−	+	−	**.729**	**−.415**	−	**7**	**984.4**	**0**	**.200**
Model 2	**1.611**	**−.488**	+	+	−	**.716**	**−.431**	−	**8**	**984.9**	**.46**	**.159**
Model 3	**1.742**	**−.493**	−	+	**.276**	**.737**	**−.416**	−	**8**	**958.3**	**.87**	**.130**

Model 4	**1.610**	**−.484**	+	+	**.250**	**.724**	**−.431**	−	**9**	**986.0**	**1.55**	**.092**
Model 5	**1.756**	**−.502**	−	+	−	**.734**	**−.415**	**−.059**	**8**	**986.4**	**1.98**	**.075**
Model 6	**1.611**	**−.492**	+	+	−	**.721**	**−.432**	**−.079**	**9**	**986.8**	**2.37**	**.061**
Model 7	**1.745**	**−.496**	−	+	−	**.745**	**−.416**	**−.109**	**9**	**987.0**	**2.59**	**.055**
Model 8	**1.608**	**−.487**	+	+	**.319**	**.733**	**−.432**	**−.124**	**10**	**987.6**	**3.18**	**.041**
Model 9	**1.678**	**−.419**	−	+	**.298**	**.801**	−	−	**6**	**988.2**	**3.76**	**.031**
Model 10	1.668	−.414	−	+	−	.811	−	−	7	989.1	4.64	.020
Model 11	1.558	−.408	+	+	.268	.794	−	−	7	989.1	4.70	.019
…												
Model 128	1.328	−.141	+	−	.368	−	−	−.141	6	1,031.7	47.23	.000
Averaged parameters:												
Estimate[a]	1.70	−.49	.09	−.54	.10	.73	−.41	−.02				
Unconditional SE	.21	.17	.15	.17	.21	.18	.19	.10				
Lower 95% CL	*1.28*	*−.83*	−.21	*−.88*	−.30	*.38*	*−.78*	−.22				
Upper 95% CL	*2.10*	*−.15*	.39	*−.21*	.51	*1.08*	*−.04*	.17				
Relative importance	−	1	.42	1	.38	1	.96	.27				

Note: The proportion of pups still alive at sampling was used as the response variable in a binomial generalized linear mixed model with a logit link function. Models within 4 AICc (Akaike information criterion corrected for small sample size) units of the best model are highlighted in bold and were used to calculate averaged effect sizes. The intercept represents a litter that was found in a solitary nest both when first found and at sampling and always stayed in the same nest box (pt. A) and was first found in a communal nest and did not move nest boxes (pt. B). Female identity and the year in which a litter was born were used as random effects. Statistically significant confidence intervals (not crossing zero) are emphasized in italic. Factors included are defined as follows: for pt. A, rearing condition = the status of a litter when first found and at sampling (com = communal; sol = solitary); relocation = a litter was relocated into a nest box different from the one in which it was first found (different nest box at sampling compared with first found); population size = the number of adults in the population during the month a litter was born; age first = a litter's age when first found (days); ls first = a litter's size when first found; mean temp = the mean temperature in the barn during the month a litter was born; for part B, no. new litters = the number of additional litters a focal litter was found with at sampling; status first = a litter's rearing condition when first found (solitary or communal); relocation = a litter was relocated into a nest box different from the one in which it was first found (different nest box at sampling compared with first found); population size = the number of adults in the population during the month a litter was born; age first = a litter's age when first found (days); ls first = a litter's size when first found; mean temp = the mean temperature in the barn during the month a litter was born. Plus signs indicate that the factor is contained in the model, and minus signs indicate that the model does not contain the factor. CL = confidence limit; w = relative model weights.

[a] Standardized on 2 standard deviations, following Gelman (2008).

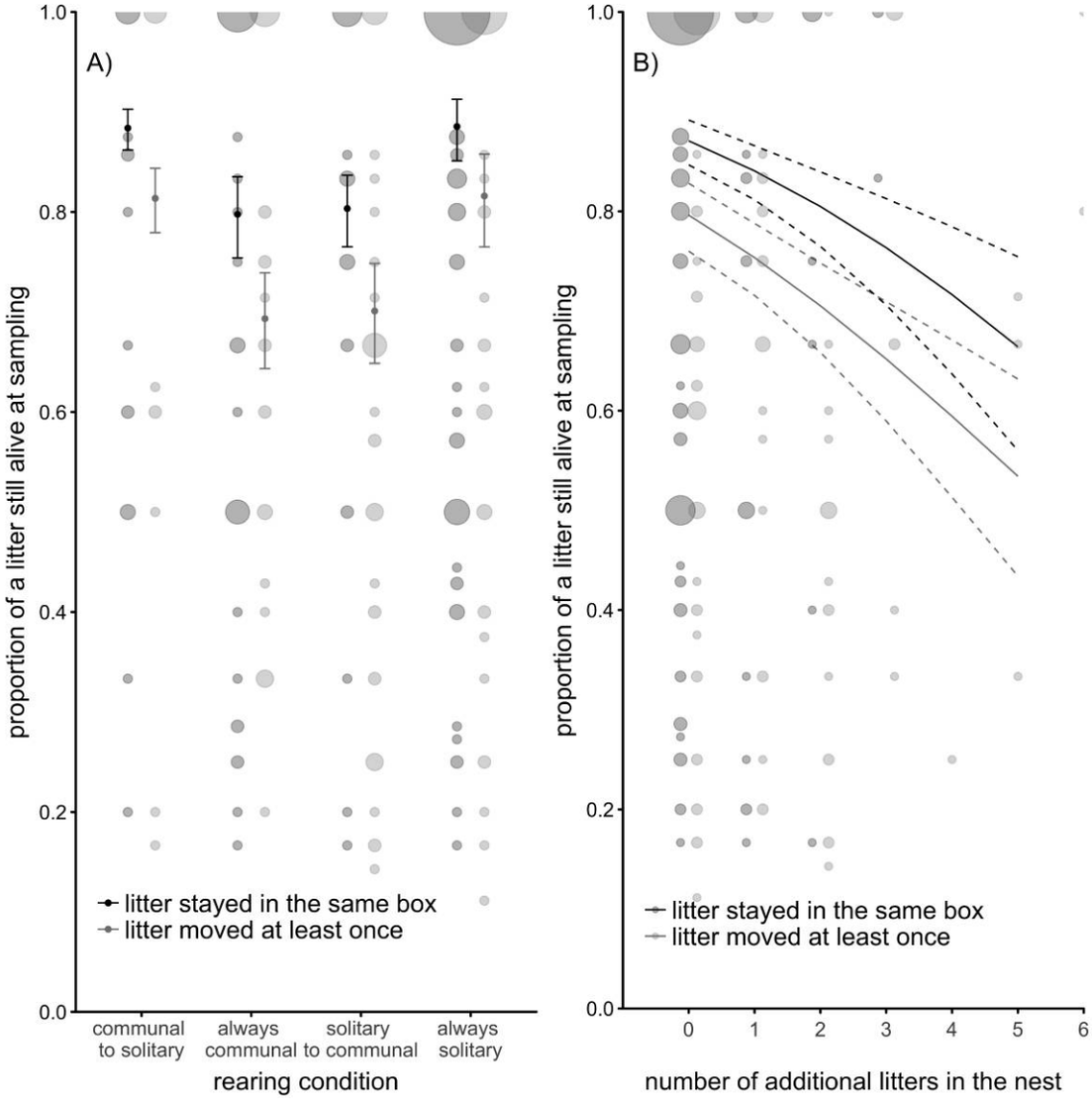

Figure 3: *A*, Proportion of pups surviving until sampling (day 13) when reared solitarily or communally (the same condition both when first found and at sampling) or in litters that were solitary when first found but communal afterward when sampled or communal when first found but solitary afterward when sampled. Dark and light gray highlight the different survival probabilities for litters that were found and sampled in the same nest box and for litters that had been moved at least once between sightings. *B*, Proportion of pups surviving until sampling in relation to the number of additional litters in the same nest box (added after a litter was first found). Plotted are model estimates (mean ± SE) obtained from model averaging of binomial generalized linear mixed models. Raw data are illustrated with circles, and the size corresponds to the sample size ($n = 340$ litters).

could not be sure that the female still cared for both parts of the litter and therefore decided to omit those cases. Additionally, some litters were removed from the analyses because of incomplete information for the factors of interest, leaving us with 852 litters.

Model selection revealed that female age was the strongest predictor of the ART used by a female. With increasing age a female's likelihood to raise pups communally decreased (fig. 4; table 5). Age correlated positively with the number of litters a female had (Pearson's correlation coefficient $= 0.60$, $P < .001$, $n = 852$); we therefore could not include female experience (number of litters) in the model as well. To disentangle whether female experience or female age caused the effect that older females reared fewer litters communally, we repeated the analysis only including a female's first litter. All females that were born and

Table 3: Model summary statistics for the recruitment analysis

	Intercept	Status at sampling	Population size	Age at sampling	ls at sampling	Mean temp	df	AICc	ΔAICc	*w*
Model 1	**−.9175**	**−**	**.5660**	**−.2787**	**.3066**	**−.4248**	**7**	**1,457.5**	**0**	**.315**
Model 2	**−.9155**	**−**	**.5239**	**−**	**.3262**	**−.4338**	**6**	**1,458.2**	**.73**	**.219**
Model 3	**−.9461**	**+**	**.5581**	**−.2689**	**.2794**	**−.4253**	**8**	**1,459.1**	**1.62**	**.140**
Model 4	**−.9505**	**+**	**.5158**	**−**	**.2928**	**−.4339**	**7**	**1,459.6**	**2.13**	**.108**
Model 5	**−.8402**	**−**	**.5554**	**−.3118**	**−**	**−.4036**	**6**	**1,461.4**	**3.98**	**.043**
Model 6	−.9115	+	.5412	−.2869	−	−.4086	7	1,461.5	4.07	.041
Model 7	.9143	+	.4951	−	−	−.4174	6	1,462.5	5.04	.025
Model 8	−.9075	+	−	−	.3181	−.3691	5	1,462.8	5.33	.022
Model 9	−.8325	+	.5075	−	−	−.4174	5	1,463.0	5.54	.020
...										
Model 32	−.9181	+	−	−	−	−	3	11,473.5	16.06	.000
Averaged parameters:										
Estimate[a]	−.92	.03	.55	−.17	.29	−.43				
Unconditional SE	.17	.09	.20	.19	.14	.12				
Lower 95% CL	*−1.26*	−.14	*.15*	−.54	*.01*	*−.67*				
Upper 95% CL	*−.58*	.20	*.94*	.20	*.57*	*−.18*				
Relative importance		.30	1	.60	.95	1				

Note: The proportion of sampled pups recruited into the population as tagged adults was used as the response variable in a binomial generalized linear mixed model with a logit link function. Models within 4 AICc (Akaike information criterion corrected for small sample size) units of the best model are highlighted in bold and were used to calculate averaged effect sizes. The intercept represents a litter that was found in a communal nest at sampling. Female identity and the year in which a litter was born were used as random effects. Statistically significant confidence intervals (not crossing zero) are emphasized in italic. Factors included are defined as follows: female tactic = rearing condition at sampling (solitary or communal); population size = the number of adults in the population during the month a litter was born; age at sampling = a litter's age at sampling (days); ls at sampling = a litter's size at sampling; mean temp = the mean temperature in the barn during the month a litter was born. Plus signs indicate that the factor is contained in the model, and minus signs indicate that the model does not contain the factor. CL = confidence limit; *w* = relative model weights.

[a] Standardized on 2 standard deviations, following Gelman (2008).

may have reproduced before 2007 were excluded from the analysis, leaving us with 237 females in the data set. Even though females had a similar level of reproductive experience because they were raising their first litter, female age still tended to affect a litter's likelihood of being raised communally or solitarily (averaged model estimate [slope] for female age: −0.60; 95% CI: −1.20 to −0.05). Age and not how many litters a female had already raised before thus seemed decisive for this effect, although we cannot entirely exclude an influence of experience. Females that reared their first litter solitarily were on average 224.2 ± 14.7 (mean ± SE) days old, while communally nursing females were on average 197.5 ± 7.2 days old.

Discussion

High allocation into reproduction, as during gestation and lactation in mammals, has been considered to create a low potential for the evolution of female ARTs. Our 5-year study of free-living house mice allowed analyzing the fitness consequences for females rearing litters either solitarily or communally and thus gaining comprehensive knowledge about the factors maintaining a rare female ART in a social rodent. More than half (54.5%) of the multiply reproducing females were observed to switch between solitary and communal nursing during their lifetime. The two tactics did not result in equal fitness (when all else was held equal). The more litters a female raised solitarily, the higher her reproductive success was (measured as the number of offspring raised until 13 days of age during her life span in the barn). Pup survival was lower in communal nests, while the mother's reproductive tactic neither affected her likelihood to reproduce again nor her interbirth interval. Our data suggest that communal and solitary nursing are two conditionally expressed alternative tactics of a single strategy. Older females (likely of larger body mass; see fig. A3) raised a higher proportion of solitary litters and gained the highest reproductive success. The younger females, on the other hand, were more likely to communally rear litters even at the cost of reduced offspring survival. With increasing age and weight, they may improve their ability to nurse litters solitarily, given they survive.

ARTs within a Single Strategy?

Half of the females reared litters both solitarily and communally during their lifetime, indicating that communal

Table 4: Model summary statistics showing the effect of pairwise relatedness, the age difference between females, and the age differences between litters on reproductive skew among mothers contributing to a communal nest

	Intercept	Age difference (females)	Age difference (litters)	Average pairwise relatedness	df	AICc	ΔAICc	*w*
Model 1	**.001**	−	−	−	**2**	**−144.4**	**.00**	**.228**
Model 2	**.001**	−	**.030**	−	**3**	**−144.3**	**.13**	**.214**
Model 3	**.015**	**.0001**	−	−	**3**	**−143.9**	**.49**	**.179**
Model 4	**.013**	**.0001**	**.026**	−	**4**	**−143.2**	**1.24**	**.123**
Model 5	**.001**	−	−	**.002**	**3**	**−142.3**	**2.16**	**.078**
Model 6	**.001**	−	**.032**	**.008**	**4**	**−142.2**	**2.20**	**.076**
Model 7	**.015**	**.0001**	−	**.003**	**4**	**−141.7**	**2.69**	**.060**
Model 8	**.013**	**.0001**	**.027**	**.009**	**5**	**−141.1**	**3.36**	**.043**
Averaged parameters:								
Estimate[a]	.006	−.00003	.013	.013				
Unconditional SE	.014	.0001	.02	.011				
Lower 95% CL	−.022	−.0001	−.03	−.02				
Upper 95% CL	.035	.0001	.05	.024				
Relative importance	−	.40	.46	.26				

Note: The binomial skew index was used as the response variable in a linear model. Models within 4 AICc (Akaike information criterion corrected for small sample size) units of the best model are highlighted in bold and were used to calculate averaged effect sizes. Statistically significant confidence intervals (not crossing zero) are emphasized in italic. Factors included are defined as follows: age difference (females) = absolute age difference (days) between the oldest and the youngest female contributing to the communal nest; age difference (litters) = age of oldest litter minus age of youngest litter (days); average pairwise relatedness = average pairwise relatedness between the females contributing to the communal nest (Wang [2002] coefficient). Minus signs indicate that the model does not contain the factor. CL = confidence limit; *w* = relative model weights.

[a] Standardized on 2 standard deviations, following Gelman (2008).

and solitary breeding are two tactics within a single strategy. Population density and the season (analyzed as the average temperature during the month a litter was raised) did not affect a litter's likelihood to be raised communally or solitarily. In general, more litters were raised communally (69% of all litters; see table 5) than solitarily and the proportion increased over time. A purely solitary strategy was rare, as it was followed by only 8% of all females that had more than one litter, and only 11% of those females' daughters also followed a purely solitary strategy. Given our observations, it seems most likely that solitary and communal breeding represent two ARTs within a single strategy. Females on average produced 2.9 litters and were increasingly likely to have used both reproductive alternatives with an increasing number of litters raised (see fig. A4), which further supports the more parsimonious explanation of two ARTs within a single strategy.

Nevertheless, we cannot exclude the existence of two genetically different strategies in the population, one being to always rear offspring solitarily and the other to perform both solitary and communal breeding. A third strategy of females exclusively rearing litters communally seems highly unlikely. Females often do not have the option to communally breed, especially at low population densities or during colonization events. Previous research on the same population reported that during an earlier period of relatively low population density (maximum density: 0.9 adults/m^2), females did not have the option for communal breeding for 42% of the litters born (Weidt et al. 2014). A later analysis of social partner choice during the years 2008 and 2009 (and thus overlapping with the study presented here) revealed that 11% of the litters were born with no other litter available in their mother's social group for communal breeding despite much higher population density (maximum density: 2.6 adults/m^2; Harrison et al. 2018).

Assuming two plastic ARTs within a single strategy, solitary litters could arise for a number of different reasons. First, a female might have been the only female breeding in her social group without an option to nurse communally, as discussed above. Second, females might not have found a social partner to their liking, therefore deciding against communal nursing, or similarly the female might not have been accepted as a cooperation partner by the other females. Previous research on the same population and at different population densities revealed that females were choosy and did not always communally nurse in the presence of another lactating group member. Instead, the more partners a female had to choose from, the more likely she was to form a communal nest, indicating that females were selective in their choice (Weidt et al. 2014; Harrison et al. 2018). This could also explain why we observed an increase in the proportion of litters raised com-

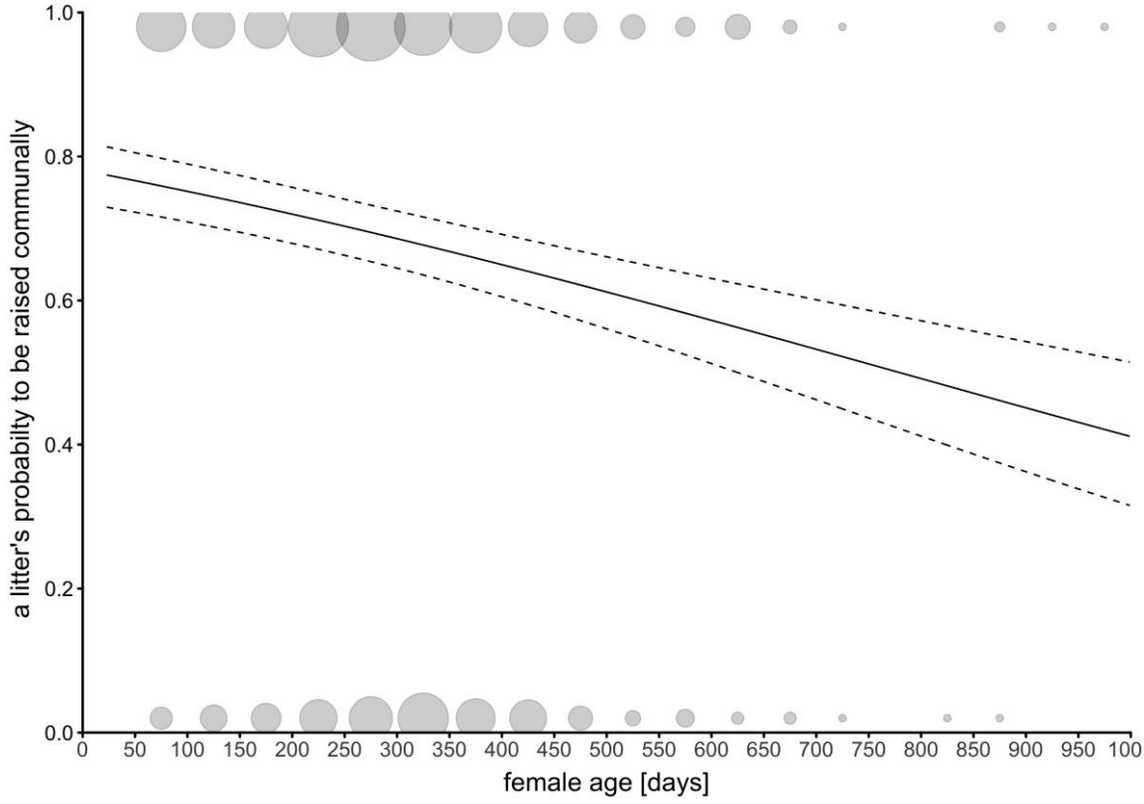

Figure 4: With increasing age, females reared fewer of their litters communally. Plotted are model estimates (mean ± SE) obtained from model averaging of binomial generalized linear mixed models. Raw data are illustrated with circles, and the size corresponds to the sample size ($n = 862$ litters). Communal litters are represented as 1, and solitary litters are represented as 0.

munally over the years, likely as a result of an increasing number of litters born (see fig. 1) and therefore also potential female partners to choose from.

It is still poorly understood how a communal nest is formed, especially in wild populations. In the laboratory, communal nests of two females occur when a highly pregnant female shares the nest with a partner already nursing a litter and adds her pups to those present in the nest. In the free-living population, several females share several nest boxes (Weidt et al. 2014; König et al. 2015), and we assume that it is the female giving birth second that decides to join a litter for communal nursing. The already-lactating female, on the other hand, may have been joined against her interest. Such a situation may exist if younger females, of relatively low body mass, are not yet competitive in monopolizing a nest box and thus in avoiding exploitation by a nonpreferred partner, as for example a female with a larger litter size. Once litters are pooled, females are unable to discriminate between their own and others' offspring and are forced to raise all litters in the communal nest or to abandon the nest (Chantrey and Jenkins 1982; König 1989; Manning et al. 1995; Ferrari et al. 2015).

Communal nursing has been described to happen preferentially among related females (Wilkinson and Baker 1988), which would reduce the costs of potentially being exploited. It was shown both theoretically and empirically (in zebra finches) that individuals are more likely to tolerate exploitation by relatives, owing to indirect fitness benefits that compensate for at least some of the costs (Mathot and Giraldeau 2010). In accordance with this, we found the pairwise relatedness (Wang estimator) between communally nursing females was on average 0.28.

If females were tolerant toward exploitation by relatives, we expected a high skew in litter sizes in communal nests (positive *B* index), suggesting that one exploits the partner(s) in terms of their drastically increased allocation to nursing nonoffspring. Females did differ in litter size and might therefore benefit unequally, but the variance in litter sizes observed within communal nests corresponded to that among all litters. Females therefore did not use infanticide to adjust a partner's litter size to their own litter size or to create a high skew.

A critical aspect here may be that we rarely know the size of a litter at birth, since we often find them when they are already several days old and therefore cannot analyze

Table 5: Model summary statistics for the factors influencing whether a litter was sampled communally or solitarily

	Intercept	Female age	Population size	Mean temp	df	AICc	ΔAICc	*w*
Model 1	**.758**	**−.380**	−	−	**4**	**1,069.1**	**.00**	**.385**
Model 2	**.759**	**−.392**	−	**−.174**	**5**	**1,070.0**	**.81**	**.257**
Model 3	**.760**	**−.385**	**−.164**	−	**5**	**1,071.0**	**1.81**	**.156**
Model 4	**.760**	**−.394**	**−.096**	**−.170**	**6**	**1,071.9**	**2.80**	**.096**
Model 5	.764	−	−	−	3	1,073.3	4.13	.049
Model 6	.764	−	−	−.146	4	1,074.4	5.29	.027
Model 7	.764	−	−.118		4	1,075.2	6.04	.019
Model 8	.765	−	−.058	−.142	5	1,076.4	7.29	.010
Averaged parameters:								
Estimate[a]	.76	−.39	−.04	−.07				
Unconditional SE	.18	.15	.20	.13				
Lower 95% CL	*.40*	*−.70*	−.43	−.32				
Upper 95% CL	*1.12*	*−.10*	.35	.19				
Relative importance		1	.28	.39				

Note: Whether a litter was sampled communally or solitarily was used as the response variable in a binomial GLMM with a logit link function. Models within 4 AICc (Akaike information criterion corrected for small sample size) units of the best model are highlighted in bold and were used to calculate averaged effect sizes. The identity of the dam of a litter (FemaleID) and the year of birth were included as random effects in all models. Statistically significant confidence intervals (not crossing zero) are emphasized in italic. Factors included are defined as follows. Female age = age of female when giving birth to the litter (days); population size = number of adults present in the barn during the month the litter was born; mean temperature = mean temperature in the barn during the month the litter was born. Minus signs indicate that the model does not contain the factor. CL = confidence limit; w = relative model weights.

[a] Standardized on 2 standard deviations, following Gelman (2008).

whether females giving birth second in a nest use infanticide to modify the skew already given by natural variance in litter sizes. Nevertheless, a laboratory study of wild derived house mice with accurate information on litter size at birth revealed no evidence that females use infanticide to equalize litter sizes; females reduced the litter size of the partner that had already given birth but did so irrespective of their own number of pups (Ferrari et al. 2016).

Fitness Consequences of Communal Nursing

We observed a large skew in reproductive success (number of offspring weaned within life span in the barn) among the females in the study population. Approximately half of the adult females did not produce pups that survived until sampling. Such a finding indicates high reproductive competition among females (Clutton-Brock 2009), one of the conditions favoring the evolution of ARTs (Taborsky et al. 2008).

Our measure for reproductive success (during the time a female lived in the barn) was limited in two ways. First, we could not quantify the actual number of pups a female weaned (onset of weaning is at an age of 17 days) but instead used the number of pups sampled per female at 13 days of age. Manning et al. (1995) never observed infanticide of pups older than 14 days in a seminatural population. Even though we slightly overestimated pup survival to weaning, our measure nevertheless covered the period of highest risk of pup infanticide. Furthermore, we do not expect factors influencing pup survival from day 1 to day 13 to differ from those impacting pups older than 13 days. While we could not measure the actual number of offspring weaned, we instead additionally analyzed how many sampled pups were recruited into the population (caught and tagged as adults). Pups that disappeared between sampling and adulthood could either have died or dispersed from the population. We observed that a mother's reproductive tactic did not affect her offsprings' probability of being recruited as adults into the population. Given the survival disadvantage of communally reared pups until sampling, solitary nursing seems also to be the more beneficial option when using the number of recruited offspring into the population as a proxy for fitness.

The second aspect limiting our estimate of reproductive success was female life span. A large fraction of females in the data set (68%) were not found dead in the barn. Instead, we only knew when they were last recorded alive in the population. Females that disappeared may have died and not been found in the barn, which we do not consider to happen frequently since we carefully check the barn during each population monitoring with handheld readers for hidden tagged corpses. Alternatively, they may have died outside the barn (eaten by predators) or dispersed and left the population with an unknown fate. We cannot exclude that some of the females survived and bred in another location, although dispersal likely is associated with high mortality and in many cases low reproductive success. We are therefore rather confident that our measure of life span and the number of offspring a female weaned represent a meaningful estimate of female reproductive success.

The strongest predictor of female reproductive success was life span. The longer a female remained in the population, the higher the number of litters she raised and consequently the higher the number of pups reaching sampling age. While this might seem unusual for species with a short life expectancy and high reproductive output, we have to keep in mind that the analyses presented here were limited to females that managed to wean at least one offspring. Future studies will have to reveal the impact of life span when considering all females, the ones that managed to reproduce, and also the ones that did not.

More intriguingly, we found that with an increasing proportion of a female's litters being raised communally, her reproductive success decreased, independent of both population size and temperature during the month she was born. One possible reason for such an effect could be different survival rates for pups raised communally and solitarily. We indeed found that the reproductive tactic used by a female correlated with pup survival. Pups raised in communal litters had a higher mortality; more specifically, each additional litter found together with the focal litter reduced its survival (irrespective of whether the litter was initially first found solitary or communal). This effect might be best explained by female infanticide, which has been described repeatedly for communally breeding female house mice (König 1994*a*; Palanza et al. 2005; Schmidt et al. 2015; Ferrari et al. 2016). Females joining a nest with an already-existing litter often kill one or several of the pups present before they give birth themselves. Alternatively, pups in large communal litters might suffer from increased pup competition, which could further reduce their survival.

Decreased offspring survival in communal nests contradicts both results from experiments in the laboratory (König 1994*a*), which found a higher reproductive success (measured over a life span of 6 months) for communally nursing females, and data from a seminatural (Manning et al. 1995) and a free-living (Auclair et al. 2014) population, which showed a higher survival for pups reared in communal nests. Both nonlaboratory studies differed from our study because they analyzed pup survival in communal nests after all females had pooled their litters. They thus likely missed infanticide occurring during or immediately before a new litter was added to a communal nest, which is consistent with the finding that litter sizes in communal nests were smaller than those in solitary nests in the Auclair et al. (2014) study. The survival benefit found by Manning et al. (1995) and Auclair et al. (2014) might, however, indicate that females raising litters communally in a natural situation can better care for the joint litter and defend it against infanticidal conspecifics. Nevertheless, when including the initial high costs of infanticide during the formation of a communal nest, as done in our study, communal nursing no longer improved pup survival but on the contrary decreased it. Improved reproductive success of communally nursing females as observed in a controlled laboratory setting, on the other hand (König 1994*a*), emphasizes the importance of observations from free-living populations. Females in a laboratory setting experience a rather "simple" and predictable social environment, with only a few familiar group members and with low female competition (over food, nesting sites, or social partners). We cannot exclude that communal nursing at very low densities in the wild might result in similar patterns. The data presented here originate from one single population, which limits the overall conclusions. Under different natural conditions—for example, under increased predation risk or with less food and/or fewer nesting sites—solitary nursing may be more costly, resulting in benefits of communal nests despite the costs of infanticide during their formation.

Conditional Reproductive Strategy

Female house mice used two ARTs and switched from one to the other, indicating that tactics are plastic. One of the two tactics (communal nursing) resulted in reduced pup survival and consequently had a negative effect on female reproductive success. Given that communal nursing reduces female reproductive success, we would expect it to be absent or decreasing in frequency; however, this is not what we observed. Communal nursing even increased in our study population, and it has been described to occur both in the laboratory and in wild populations (Sayler and Salmon 1971; Manning et al. 1995; König 2006; Weidt et al. 2014). Weidt et al. (2014) further showed that communal nursing did not necessarily increase with population size and that females still raised litters solitarily in situations where they had the opportunity to form communal nests within their social groups, indicating it is not simply a by-product of group living. Taken together, these findings suggest that the reproductive tactic of nursing litters communally is beneficial in specific situations.

The occurrence of two ARTs with on average unequal fitness outcomes can best be explained by a condition-dependent strategy (Taborsky et al. 2008). Condition-dependent ARTs are often characterized by individuals differing in competitive abilities (Gross 1996) and showing plasticity in choosing a tactic depending on their condition. Hence, we hypothesize that females might not always be able to rear their litters solitarily and instead opt for communal nursing, even at the cost of reduced pup survival. Younger females might not be able to efficiently protect their young against infanticide by nongroup members, which is rather common in house mice (vom Saal 1984; Manning et al. 1995; Auclair et al. 2014). Alternatively, younger females might be unable to prevent other females from joining, therefore being exploited when communally nursing their litters.

The alternative for such females would be not to reproduce at all or to delay reproduction that might be associated with even higher costs in a species experiencing low life expectancy (Manser et al. 2011). We find that age affected a female's likelihood to rear a litter communally, indicating that body condition indeed influenced the reproductive tactic of a female. Females increased in body mass when getting older (see fig. A3), so weight and not age may have driven the effect. Heavier females are able to produce more milk (Ferrari et al. 2015) and likely are also better competitors in aggressive encounters. Body mass or body size were found to influence condition-dependent ARTs in various species, both in males (Tomkins and Brown 2004; Painting and Holwell 2014) and in females (Hill et al. 2015).

Conclusions

Communal nursing has been reported for different rodent species and has often been associated with reduced reproductive success for the females involved (Gerlach and Bartmann 2002; Lacey 2004; Hayes et al. 2009). Condition-dependent ARTs can explain those findings and have been suggested to be of importance in African striped mice (*Rhabdomys pumilio*; Hill et al. 2015). Analyzing and interpreting an apparently mutualistically beneficial behavior as communal offspring care under the framework of condition-dependent ARTs contributes to our understanding of how it is maintained in a population despite its fitness costs. In such a scenario, we would not expect selection for one or the other behavior (strategy); rather, we would expect selection for the appropriate reaction norm, allowing individuals to choose the optimal tactic given the circumstances. Further research should therefore more strongly focus on deepening our understanding of the evolution of phenotypic plasticity and its role in cooperation. Including in such analyses female-female competition and female social partner choice will add to the exciting discussion of how the social environment modifies individual behavior.

Acknowledgments

We thank Jari Garbely for genetic laboratory work and genotype scoring, Corinne Ackermann for her contribution to the parentage analysis, and Gabriele Stichel, Sally Steinert, and Bruce Boatman for animal caretaking. Furthermore, we thank all former and current members of the mouse group for the data collection. The long-term collection of data on wild house mice and therefore also this study were financially supported by the Claraz Stiftung, the Foundation for Research in Science and the Humanities at the University of Zurich, the Promotor Stiftung, the Julius-Klaus Stiftung, and the Swiss National Science Foundation (grants 120444 and 31003A_176114/1).

Literature Cited

Ahlund, M., and M. Andersson. 2001. Brood parasitism: female ducks can double their reproduction. Nature 414:600–601.

Auclair, Y., B. König, and A. K. Lindholm. 2014. Socially mediated polyandry: a new benefit of communal nesting in mammals. Behavioral Ecology 25:1467–1473.

Bartoń, K. 2014. MuMIn: multi-model inference. R package version 1.10.0.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2014. lme4: linear mixed-effects models using Eigen and S4. Journal of Statistical Software 67:1–48. R package version 1.1-7.

Brockmann, H. J. 2008. Alternative reproductive tactics in insects. Pages 177–223 *in* R. F. Oliveira, H. J. Brockmann, and M. Taborsky, eds. Alternative reproductive tactics: an integrative approach. Cambridge University Press, Cambridge.

Brockmann, H. J., A. Grafen, and R. Dawkins. 1979. Evolutionarily stable nesting strategy in a digger wasp. Journal of Theoretical Biology 77:473–496.

Brown, C. R., and M. B. Brown. 1998. Fitness components associated with alternative reproductive tactics in cliff swallows. Behavioral Ecology 9:158–171.

Bult, C. J., J. T. Eppig, J. A. Kadin, J. E. Richardson, and J. A. Blake. 2007. The Mouse Genome Database (MGD): mouse biology and model systems. Nucleic Acids Research 36:D724–D728.

Chantrey, D. F., and B. Jenkins. 1982. Sensory processes in the discrimination of pups by female mice (*Mus musculus*). Animal Behaviour 30:881–885.

Clutton-Brock, T. H. 2009. Sexual selection in females. Animal Behaviour 77:3–11.

Dobay, A., P. Pilo, A. K. Lindholm, F. Origgi, H. C. Bagheri, and B. König. 2015. Dynamics of a tularemia outbreak in a closely monitored free-roaming population of wild house mice. PLoS ONE 10:e0141103.

Ferrari, M., and B. König. 2017. No evidence for punishment in communally nursing female house mice (*Mus musculus domesticus*). PLoS ONE 12:e0179683.

Ferrari, M., A. K. Lindholm, and B. König. 2015. The risk of exploitation during communal nursing in house mice, *Mus musculus domesticus*. Animal Behaviour 110:133–143.

———. 2016. A reduced propensity to cooperate under enhanced exploitation risk in a social mammal. Proceedings of the Royal Society B 283:20160068.

———. 2018. Data from: Fitness consequences of female alternative reproductive tactics in house mice (*Mus musculus domesticus*). American Naturalist, Dryad Digital Repository, doi:10.5061/dryad.k1s0c7h.

Field, J. 1992. Intraspecific parasitism as an alternative reproductive tactic in nest-building wasps and bees. Biological Reviews 67:79–126.

———. 1994. Selection of host nests by intraspecific nest-parasitic digger wasps. Animal Behaviour 48:113–118.

Gelman, A. 2008. Scaling regression inputs by dividing by two standard deviations. Statistics in Medicine 27:2865–2873.

Gerlach, G., and S. Bartmann. 2002. Reproductive skew, costs, and benefits of cooperative breeding in female wood mice (*Apodemus sylvaticus*). Behavioral Ecology 13:408–418.

Gross, M. R. 1996. Alternative reproductive strategies and tactics: diversity within sexes. Trends in Ecology and Evolution 11:92–98.

Grueber, C., S. Nakagawa, R. Laws, and I. Jamieson. 2011. Multimodel inference in ecology and evolution: challenges and solutions. Journal of Evolutionary Biology 24:699–711.

Hager, R., and C. B. Jones. 2009. Reproductive skew in vertebrates: proximate and ultimate causes. Cambridge University Press, Cambridge.

Harrison, N., A. K. Lindholm, A. Dobay, O. Halloran, A. Manser, and B. König. 2018. Female nursing partner choice in a population of wild house mice (*Mus musculus domesticus*). Frontiers in Zoology 15:4.

Hayes, D. L., A. S. Chesh, R. A. Castro, L. O. Tolhuysen, J. R. Burger, J. Bhattacharjee, and L. A. Ebensperger. 2009. Fitness consequences of group living in the degu *Octodon degus*, a plural breeder rodent with communal care. Animal Behaviour 78:131–139.

Hill, D. L., N. Pillay, and C. Schradin. 2015. Alternative reproductive tactics in female striped mice: heavier females are more likely to breed solitarily than communally. Journal of Animal Ecology 84:1497–1508.

Kalinowski, S. T., M. L. Taper, and T. C. Marshall. 2007. Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. Molecular Ecology 16:1099–1106.

König, B. 1989. Kin recognition and maternal care under restricted feeding in house mice (*Mus domesticus*). Ethology 82:328–343.

———. 1993. Maternal investment of communally nursing female house mice (*Mus musculus domesticus*). Behavioural Processes 30:61–74.

———. 1994*a*. Components of lifetime reproductive success in communally and solitarily nursing house mice: a laboratory study. Behavioral Ecology and Sociobiology 34:275–283.

———. 1994*b*. Fitness effects of communal rearing in house mice: the role of relatedness versus familiarity. Animal Behaviour 48:1449–1457.

———. 2006. Non-offspring nursing in mammals: general implications from a case study on house mice. Pages 191–205 *in* P. M. Kappeler and C. P. van Schaik, eds. Cooperation in primates and humans: mechanisms and evolution. Springer, Berlin.

König, B., and A. K. Lindholm. 2012. The complex social environment of female house mice (*Mus domesticus*). Pages 114–134 *in* M. Macholàn, S. J. E. Baird, P. Mundlinger, and J. Piàlek, eds. Evolution of the house mouse. Cambridge University Press, Cambridge.

König, B., A. K. Lindholm, P. C. Lopes, A. Dobay, S. Steinert, and F. J.-U. Buschmann. 2015. A system for automatic recording of social behavior in a free-living wild house mouse population. Animal Biotelemetry 3:1–15.

Lacey, E. A. 2004. Sociality reduces individual direct fitness in a communally breeding rodent, the colonial tuco-tuco (*Ctenomys sociabilis*). Behavioral Ecology and Sociobiology 56:449–457.

Lank, D. B., C. M. Smith, O. Hanotte, T. Burke, and F. Cooke. 1995. Genetic polymorphism for alternative mating behaviour in lekking male ruff *Philomachus pugnax*. Nature 378:59–62.

Lidicker, W. Z. 1976. Social behaviour and density regulation in house mice living in large enclosures. Journal of Animal Ecology 45:677–697.

Lopes, P. C., P. Block, and B. König. 2016. Infection-induced behavioural changes reduce connectivity and the potential for disease spread in wild mice contact networks. Scientific Reports 6:31790.

Lyon, B. E. 1993. Conspecific brood parasitism as a flexible female reproductive tactic in American coots. Animal Behaviour 46:911–928.

Manning, C. J., D. A. Dewsbury, E. K. Wakeland, and W. K. Potts. 1995. Communal nesting and communal nursing in house mice, *Mus musculus domesticus*. Animal Behaviour 50:741–751.

Manser, A., A. K. Lindholm, B. König, and H. C. Bagheri. 2011. Polyandry and the decrease of a selfish genetic element in a wild house mouse population. Evolution 65:2435–2447.

Mathot, K. J., and L.-A. Giraldeau. 2010. Within-group relatedness can lead to higher levels of exploitation: a model and empirical test. Behavioral Ecology 21:843–850.

McGuire, B., and L. L. Getz. 2010. Alternative male reproductive tactics in a natural population of prairie voles *Microtus ochrogaster*. Acta Theriologica 55:261–270.

Mikesic, D. G., and L. C. Drickamer. 1992. Factors affecting home-range size in house mice (*Mus musculus domesticus*) living in outdoor enclosures. American Midland Naturalist 127:31–40.

Nonacs, P. 2000. Measuring and using skew in the study of social behavior and evolution. American Naturalist 156:577–589.

———. 2003. Measuring the reliability of skew indices: is there one best index? Animal Behaviour 65:615–627.

Painting, C. J., and G. I. Holwell. 2014. Flexible alternative mating tactics by New Zealand giraffe weevils. Behavioral Ecology 25:1409–1416.

Palanza, P., D. Della Seta, P. F. Ferrari, and S. Parmigiani. 2005. Female competition in wild house mice depends upon timing of female/male settlement and kinship between females. Animal Behaviour 69:1259–1271.

R Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Sayler, A., and M. Salmon. 1969. Communal nursing in mice: influence of multiple mothers on the growth of the young. Science 164:1309–1310.

———. 1971. An ethological analysis of communal nursing by the house mouse (*Mus musculus*). Behaviour 40:62–85.

Schmidt, J., A. Kosztolányi, J. Tökölyi, B. Hugyecz, I. Illés, R. Király, and Z. Barta. 2015. Reproductive asynchrony and infanticide in house mice breeding communally. Animal Behaviour 101:201–211.

Schradin, C., and A. K. Lindholm. 2011. Relative fitness of alternative male reproductive tactics in a mammal varies between years. Journal of Animal Ecology 80:908–917.

Schradin, C., A. K. Lindholm, J. Johannesen, I. Schoepf, C.-H. Yuen, B. König, and N. Pillay. 2012. Social flexibility and social evolution in mammals: a case study of the African striped mouse (*Rhabdomys pumilio*). Molecular Ecology 21:541–553.

Scott, M. P., and S. M. Williams. 1993. Comparative reproductive success of communally breeding burying beetles as assessed by PCR with randomly amplified polymorphic DNA. Proceedings of the National Academy of Sciences of the USA 90:2242–2245.

Shuster, S. M. 2008. The expression of crustacean mating system strategies. Pages 224–250*in* R. F. Oliveira, H. J. Brockmann, and M. Taborsky, eds. Alternative reproductive tactics: an integrative approach. Cambridge University Press, Cambridge.

Shuster, S. M., and M. J. Wade. 1991. Equal mating success among male reproductive strategies in a marine isopod. Nature 350:608–610.

Stockley, P., and J. Bro-Jørgensen. 2011. Female competition and its evolutionary consequences in mammals. Biological Reviews 86:341–366.

Taborsky, M., R. F. Oliveira, and H. J. Brockmann. 2008. The evolution of alternative reproductive tactics: concepts and questions. Pages 1–22 *in* R. F. Oliveira, H. J. Brockmann, and M. Taborsky, eds. Alternative reproductive tactics: an integrative approach. Cambridge University Press, Cambridge.

Teschke, M., O. Mukabayire, T. Wiehe, and D. Tautz. 2008. Identification of selective sweeps in closely related populations of the house mouse based on microsatellite scans. Genetics 180:1537–1545.

Tomkins, J. L., and G. S. Brown. 2004. Population density drives the local evolution of a threshold dimorphism. Nature 431:1099–1103.

vom Saal, F. S. 1984. Proximate and ultimate causes of infanticide and parental behaviour in male house mice. Pages 401–424 *in* G. Hausfater and S. Hrdy, eds. Infanticide: comparative and evolutionary perspectives. Aldine Transaction, Piscataway, NJ.

Wang, J. 2002. An estimator for pairwise relatedness using molecular markers. Genetics 160:1203–1215.

———. 2011. Coancestry: a program for simulating, estimating and analysing relatedness and inbreeding coefficients. Molecular Ecology Resources 11:141–145.

Weidt, A., A. K. Lindholm, and B. König. 2014. Communal nursing in wild house mice is not a by-product of group living: females choose. Naturwissenschaften 101:73–76.

Wilkinson, G. S., and A. M. Baker. 1988. Communal nesting among genetically similar house mice. Ethology 77:103–114.

Yanagisawa, Y. 1985. Parental strategy of the cichlid fish *Perissodus microlepis*, with particular reference to intraspecific brood "farming out." Environmental Biology of Fishes 12:241–249.

Yom-Tov, Y. 1980. Intraspecific nest parasitism in birds. Biological Reviews 55:93–108.

Zink, A. G. 2003. Intraspecific brood parasitism as a conditional reproductive tactic in the treehopper *Publilia concava*. Behavioral Ecology and Sociobiology 54:406–415.

Associate Editor: Jean-Michel Gaillard
Editor: Yannis Michalakis

Free-living house mice (*Mus musculus domesticus*). Photo credit: Barbara König.